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Scale dependence of ecological assembly rules: Insights from empirical datasets and joint species distribution modelling

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Abstract

1. A comprehensive understanding of the scale dependency of environmental filtering and biotic interactions influencing the local assembly of species is paramount to derive realistic forecasts of the future of biodiversity and efficiently manage ecological communities. A classical assumption is that environmental filters are more prevalent at coarser scales with diminishing effects towards the finest scales where biotic interactions become more decisive. Recently, a refinement was proposed stipulating that the scale dependency of biotic interactions should relate to the type of interaction. Specifically, the effect of negative interactions (e.g. competition) should diminish with coarsening scale, whereas positive interactions (i.e. facilitation) should be detected irrespective of the scale.
2. We use multiple vascular plant species datasets sampled at nested spatial scales (plot size varying from 0.04 to 64 m²) and recently developed joint species distribution models to test the hypotheses.
3. Our analyses indicate slightly stronger environmental filtering with increasing plot size. While the overall strength of biotic interactions did not vary consistently across scales, we found a tendency for negative interactions to fade away with increasing plot size slightly more than positive interactions.
4. *Synthesis.* We provide partial, but not unambiguous, evidence of the scale dependency of ecological assembly rules. However, our correlative methodology only allows us to interpret the findings as indication of environmental filtering and biotic interactions.

KEYWORDS

Alps, Arctic, biotic interactions, co-occurrence, environmental and residual correlation, environmental filtering, local plant community, positive and negative associations

1 | INTRODUCTION

Environmental filtering and biotic interactions are known to jointly rule the assembly of species into local communities from a regional species pool defined by historical contingencies and dispersal (Götzenberger et al., 2012; Lortie et al., 2004; Vellend, 2010). These ecological

assembly rules are hypothesized to function hierarchically at different spatial scales (Hart, Usinowicz, & Levine, 2017; McGill, 2010; Pearson & Dawson, 2003; Schneider, 2001; Thuiller, Pollock, Gueguen, & Münkemüller, 2015; Wiens, 1989). Species with abilities to access the site and presenting ecological requirements that match the specific local abiotic conditions (i.e. environmental filtering) are candidates

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for the next filter, biotic interactions, expected to function among close neighbours. At these finest spatial scales, for instance, competitively superior species may inhibit the existence of species with lower capacity to compete for resources (Klausmeier & Tilman, 2002; Passarge & Huisman, 2002), or the close spatial proximity with other species may have positive influences through facilitative interactions (Brooker et al., 2008; Bruno, Stachowicz, & Bertness, 2003; Stachowicz, 2001). However, empirical evidence so far has not consistently supported scale dependency of ecological assembly rules (e.g. Firth & Crowe, 2010). In particular, it remains unclear whether biotic interactions affect species co-occurrence patterns at coarse spatial scales (Araújo & Luoto, 2007; Belmaker et al., 2015; Gotelli, Graves, & Rahbek, 2010; Wisz et al., 2013; Yackulic, 2017) or if, in contrast, their effect is averaged out (Godsoe, Murray, & Plank, 2015; Hui, 2009; Segurado, Kunin, Filipe, & Araújo, 2012; Thuiller et al., 2015).

Recently, Araújo and Rozenfeld (2014) developed a mathematical model, which postulates that the scale dependency of biotic interactions depends on the type of interaction. According to this model, positive interactions between species, such as mutualism and commensalism, manifest at all spatial scales, while the effect of negative interactions should diminish as the resolution gets coarser (Figure 1). The reasoning behind this model is simple. Positive interactions sustain across different spatial resolutions because if species are co-occurring due to facilitation they appear together at all scales of observations (Araújo & Luoto, 2007). Negative interactions leading to local extinctions, in contrast, might not be apparent at coarser scales where increase in space allows the coexistence of competitive species without too close proximity (Conti, de Bello, Lepš, Acosta, & Carboni, 2017; Godsoe et al., 2015). However, empirical studies conducted so far found little support for these expectations (e.g. Belmaker et al., 2015).

The traditional methodology to infer species associations deviating from random patterns (proxy for biotic interactions) consists

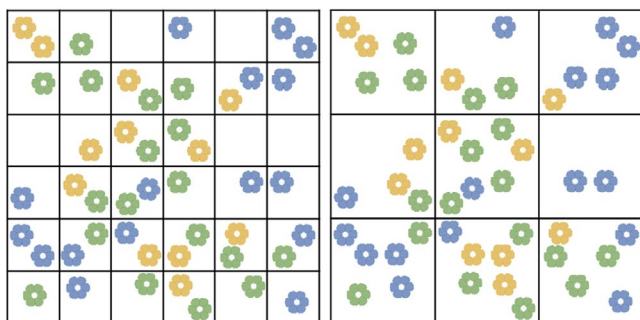


FIGURE 1 At fine spatial resolution (i.e. small plot size on the left), yellow and green species occur more often together than alone indicating a positive association, whereas yellow and blue species rarely occur together indicating a negative association. At coarse spatial resolution (i.e. large plot size on the right), yellow and green species occur together more often than alone indicating a positive association similar as in fine scale, whereas yellow and blue species now also indicate a positive association due to more frequent co-occurrence enabled by increasing plot size [Colour figure can be viewed at wileyonlinelibrary.com]

in analysing species co-occurrence matrices using different types of null model approaches (Gotelli, 2000; Gotelli & McCabe, 2002; Götzenberger et al., 2012). While these approaches make it possible to study pairwise interactions at the community level, they make it difficult to discern if non-random species associations result from biotic interactions, species' environmental preferences or dispersal processes (Chalmandrier et al., 2013; D'Amen, Mod, Gotelli, & Guisan, 2018). For example, segregated patterns could be caused by competition (Gutiérrez, Boria, & Anderson, 2014), environmental filtering (Firth & Crowe, 2010) or dispersal limitations (García-Valdés, Gotelli, Zavala, Purves, & Araújo, 2015). To overcome this challenge, one can use methods that account for environmental conditions and/or dispersal in driving species co-occurrences (e.g. constrained modelling or ordination analyses; D'Amen et al., 2018; Peres-Neto, Olden, & Jackson, 2001). A recent implementation of such approach is joint species distribution modelling (JSDM), which is based on a hierarchical model composed of two stages (Warton et al., 2015; Wilkinson, Golding, Guillera-Arroita, Tingley, & McCarthy, 2019). The first stage fits a GLM to multiple species simultaneously to account for the effects of environmental factors. In the second stage, the residuals of the fitted models are used to infer species associations not explained by the considered environmental variables. Thus, JSDMs can be used to disentangle the degree with which non-random associations between species might be driven by environmental filtering (species pairs with correlated environmental responses) and biotic interactions (species pairs with correlated model residuals; Pollock et al., 2014; Zurell, Pollock, & Thuiller, 2018). While JSDMs have been used in this context (e.g. D'Amen et al., 2018), it is important to note that JSDM is a correlative approach (Dormann et al., 2012) and that residual correlations may also appear due to missing (environmental) covariate that influence species co-occurrences (Hui, 2016; Pollock et al., 2014). It should thus be clear that JSDMs can nominate possible environmental filtering and biotic interactions but do not provide unequivocal evidence for them.

Understanding how and to which extent environmental filtering and biotic interactions shape ecological communities at different spatial scales is paramount to forecast future changes at different biodiversity levels and set-up efficient management strategies (Guisan & Rahbek, 2011; Heller & Zavaleta, 2009; Kremen, 2005; Levin, 1992; Wainwright et al., 2018). Here, we aim to examine the scale dependency of environmental filtering and biotic interactions influencing assembly of local vascular plant communities using four datasets collected in alpine (Swiss Alps) and arctic (northern Finland) environments. Due to the relatively small extents of the two study areas, the species can be assumed free of dispersal limitations (D'Amen et al., 2018; Pottier et al., 2013; le Roux, Lenoir, Pellissier, Wisz, & Luoto, 2013). In each dataset, species data were sampled within multiple nested plot sizes (i.e. spatial resolutions; sensu scale in Araújo & Rozenfeld, 2014; see also Dungan et al., 2002). Plot sizes varied from 20×20 cm (0.04 m²) to 8×8 m (64 m²); a resolution at which herbaceous species can effectively have an impact on each other, yet sampling is still feasible (Stoll & Weiner, 2000). Methodologically, we make benefit of JSDMs (Warton et al., 2015)

by fitting one model for each plot size within each dataset. Based on the models, we assess segregation and aggregation of species pairs, whether these associations are likely driven by environmental filtering and/or putative biotic interactions, and how the pairwise species associations and their potential drivers vary across spatial scales.

2 | MATERIALS AND METHODS

2.1 | Datasets

We examined species pairwise associations across spatial scales using different datasets collected in non-forested sites from two study areas. Each dataset comprises presence-absence observations of all vascular plant species sampled at various nested plot sizes (varying from $20 \times 20 \text{ cm} = 0.04 \text{ m}^2$ to $8 \times 8 \text{ m} = 64 \text{ m}^2$) together with spatially related information on the abiotic environment (Table 1). Species were recorded as present even if only a part of above-ground vegetative growth was within the plot. To ensure reliable model parameter estimation, only species with prevalence of 5–95 % at all plot sizes for a given dataset were retained for statistical analyses, (Figures S1 and S2 in Appendix). For each dataset, we selected the environmental variables based on previous studies (e.g. Dubuis et al., 2013; le Roux, Aalto, & Luoto, 2013) showing that they comprehensively represent the eco-physiological requirements of plant species in the study areas: temperature, moisture, soil and light conditions (Mod, Scherrer, Luoto, & Guisan, 2016).

The first dataset (AlpineM) was collected in the western Swiss Alps ($46^{\circ}23'N$, $7^{\circ}5'E$; e.g. Randin et al., 2006; Randin, Jaccard, Vittoz, Yoccoz, & Guisan, 2009) and consists of 434 sites, each with four nested square plots of 1, 4, 16 and 64 m^2 (Table 1; Figure S3 in the Appendix). Minimum and maximum distances among sites are 200 m and 40 km, respectively, covering an elevation gradient of 375–3,210 m a.s.l. The dataset has a total of 910 species, but only 122 species met our prevalence criteria, while 420 sites presented at least one species across all resolutions (Table 1; Figure S1 in Appendix). The environmental variables (growing degree days, topographic position index, soil pH and solar radiation) for each site were derived from raster layers with a spatial resolution of $25 \times 25 \text{ m}$. Resolution of the environmental data was considered to be appropriate with regard to the topographic variability in the study area (Pradervand, Dubuis, Pellissier, Guisan, & Randin, 2014). See Zimmermann and Roberts (2001), Randin et al. (2006) and Buri et al. (2017) for a detailed description of the abiotic variables.

The second dataset (AlpineCM) comes from the same study area in the Swiss Alps, but consists of a different and spatially independent dataset of 298 square sites of 4 m^2 (see Pottier et al., 2013), with additional five square subplots of $20 \times 20 \text{ cm}$ within each site (Figure S4 in Appendix; Scherrer et al., 2019). Minimum and maximum distances between the sites are 113 m and 40 km, respectively, with elevation ranging from 818 to 3,045 m a.s.l. This dataset has a total species number of 725, but after applying our prevalence criteria, and removing the sites with no species, 52 species and 274 sites with 1,305 subplots were retained for statistical analyses (Table 1;

TABLE 1 Details of the used datasets sampled in the Swiss Alps (AlpineM and AlpineCM) and in northern Finland (ArcticCM and ArcticM). ArcticM_{env16} and ArcticM₂₁₀ are additional datasets used to test for the influence of grain size of abiotic predictors and number of sites respectively

Dataset	Plot sizes	Grain size of abiotic predictors	Number of plots	Number of species	M (SD) prevalence of species (%)
AlpineM	$1 \times 1 \text{ m} = 1 \text{ m}^2$	$25 \times 25 \text{ m}$	420	122	13.4 (9.7)
	$2 \times 2 \text{ m} = 4 \text{ m}^2$	$25 \times 25 \text{ m}$	420	122	17.2 (11.2)
	$4 \times 4 \text{ m} = 16 \text{ m}^2$	$25 \times 25 \text{ m}$	420	122	20.5 (12.1)
	$8 \times 8 \text{ m} = 64 \text{ m}^2$	$25 \times 25 \text{ m}$	420	122	24.3 (12.8)
AlpineCM	$20 \times 20 \text{ cm} = 0.04 \text{ m}^2$	$25 \times 25 \text{ m}$	1,305	52	12.7 (8.1)
	$200 \times 200 \text{ cm} = 4 \text{ m}^2$	$25 \times 25 \text{ m}$	274	52	27.8 (13.8)
ArcticCM	$20 \times 20 \text{ cm} = 0.04 \text{ m}^2$	$1 \times 1 \text{ m}$	1,863	27	19.7 (18.9)
	$40 \times 40 \text{ cm} = 0.16 \text{ m}^2$	$1 \times 1 \text{ m}$	1,863	27	26.3 (20.9)
	$100 \times 100 \text{ cm} = 1 \text{ m}^2$	$1 \times 1 \text{ m}$	1,863	27	35.5 (21.9)
ArcticM	$1 \times 1 \text{ m} = 1 \text{ m}^2$	$1 \times 1 \text{ m}$	3,321	48	18.4 (14.5)
	$2 \times 2 \text{ m} = 4 \text{ m}^2$	$2 \times 2 \text{ m}$	839	48	26.8 (17.3)
	$4 \times 4 \text{ m} = 16 \text{ m}^2$	$4 \times 4 \text{ m}$	210	48	37.6 (20.5)
ArcticM _{env16}	$1 \times 1 \text{ m} = 1 \text{ m}^2$	$4 \times 4 \text{ m}$	3,321	48	18.4 (14.5)
	$2 \times 2 \text{ m} = 4 \text{ m}^2$	$4 \times 4 \text{ m}$	839	48	26.8 (17.3)
	$4 \times 4 \text{ m} = 16 \text{ m}^2$	$4 \times 4 \text{ m}$	210	48	37.6 (20.5)
ArcticM ₂₁₀	$1 \times 1 \text{ m} = 1 \text{ m}^2$	$1 \times 1 \text{ m}$	210	48	18.5 (15.0)
	$2 \times 2 \text{ m} = 4 \text{ m}^2$	$2 \times 2 \text{ m}$	210	48	26.1 (17.3)
	$4 \times 4 \text{ m} = 16 \text{ m}^2$	$4 \times 4 \text{ m}$	210	48	37.4 (20.8)

Figure S1 in Appendix). The environmental data were the same as for the previous dataset.

The remaining datasets were collected from square plots of different resolutions in mount Saana in northern Finland (69°2'N, 20°51'E; ~600–800 m a.s.l.). The plots are situated above the tree line and organized in 21 grids of 8 × 20 m, each grid consisting of 160 plots of 1 m² (Aalto, Scherrer, Lenoir, Guisan, & Luoto, 2018; Figures S5–S7 in Appendix). The minimum and maximum distances between grids are 20 m and 3.2 km respectively. The first arctic dataset (ArcticCM) contains 12 grids (see le Roux, Aalto, et al., 2013; le Roux, Pellissier, Wisz, & Luoto, 2014) with species sampled within plots of sizes 20 × 20, 40 × 40 and 100 × 100 cm (Figure S5 in Appendix). Under this design, plots of 20 and 40 cm resolutions are nested and randomly located inside the 100 cm plots. The total species richness of this dataset amounts to 114 species but only 27 species (within 1,863 sites) met our prevalence criteria (Table 1; Figure S2 in Appendix). For this dataset, we derived abiotic variables (soil temperature, moisture and pH, annual solar radiation and rock cover) at a 1 × 1 m resolution to reflect the heterogeneity of the landscape (le Roux, Aalto, et al., 2013; le Roux, Lenoir, et al., 2013). For a detailed description of the dataset and the sampling procedures, in addition to above-cited literature, see Aalto, le Roux, and Luoto (2013) and le Roux and Luoto (2014).

The second Arctic dataset (ArcticM) comprises all 21 grids. Here, 1 m² is used as the smallest plot size, and species data with larger plot sizes (4 and 16 m²) were formed by dividing the grids into 2 × 2 m and 4 × 4 m plots (Figure S6 in Appendix). This resulted in 3,360, 840 and 210 plots with resolutions of 1, 4 and 16 m² respectively (Table 1). After applying our prevalence criteria, total species richness decreased from 134 to 48 species. Additionally, few plots of 1 and 4 m² containing no species were removed. This dataset was modelled with the same environmental variables as for the ArcticCM dataset, but for plots of 2 × 2 m and 4 × 4 m, we used the mean (median for pH) environmental values of the corresponding 1 × 1 m plots.

2.2 | Statistical analyses

Pairwise species associations and their potential causes were analysed using multivariate Bayesian JSDM as implemented in the R-package BORAL (Hui, 2016). A key feature of this JSDM is the ability to incorporate latent variables as a parsimonious model-based ordination to assess correlation between species. The model is fitted in hierarchical manner. First, *boral* assess environmental responses of each species by fitting a GLM, by regressing a $n \times p$ matrix where rows $i = 1, \dots, n$ are sites and columns $j = 1, \dots, p$ are species recorded at each site against a $n \times q$ matrix where columns $k = 1, \dots, q$ are the values of environmental variables measured at each site. Then, species pairwise associations, not explained by the used environmental factors, are assessed as correlation of model residuals. This is done by incorporating latent variables, and residual correlations are derived from the loadings of the latent variables (Ovaskainen et al., 2017). Although the use of latent variables could imply a loss of information, the reduction of the number of parameters to be estimated leads to a considerably reduced computational burden and it has been shown that similar estimates are usually obtained relative to other methods (Wilkinson et al., 2019). Overall, while the spirit of the BORAL package is ordination based, environmental and residual correlations are estimated based on the parameters estimated from the model and can thus be related to the data-generating process (Hui, Taskinen, Pledger, Foster, & Warton, 2015).

The associations among the species pairs and their potential causes are then derived from the correlations of environmental responses (i.e. species pairs associated due to environmental filtering) and correlations of model residuals (i.e. species pairs associated due to other factors; potentially biotic interactions). For example, a positive environmental correlation and a negative residual correlation suggest that the two species are competitors owing to a similar environmental niche, whereas both positive environmental and residual correlations suggest that the two species share a similar environmental niche and potentially facilitates each other's occurrence. For interpretations of all combinations of environmental and residual correlations, see Table 2.

TABLE 2 Ecological interpretation of different combinations of environmental and residual correlations. Note that due to the correlative nature of joint species distribution models (JSDMs), identified associations only suggest causal ecological process (i.e. environmental filtering and biotic interactions). Residual correlations, in particular, could be related to a missing (environmental) factor that influence distribution of both species in a pair

		Environmental correlations		
		Negative	Random	Positive
Residual correlations	Positive	Species pair with different response to environmental conditions and potential facilitation where they co-occur	Facilitating species pair (or species often occurring together due e.g. to a missing factor)	Facilitating species pair presenting similar response to environmental conditions
	Random	Species pair with different response to environmental conditions (segregation explained by environmental filtering only)	Randomly associated species pair (neutral or stochastic processes)	Species pair with similar response to environmental conditions (aggregation explained by environmental filtering only) or mutualism
	Negative	Species pair with different response to environmental conditions and potential competition in parts of niches where they co-occur	Competing species pair (or a species rarely occurring together due e.g. to a missing factor)	Competing species pair with similar response to environmental conditions

Parameter estimation was obtained using iterative sampling based on a Monte Carlo Markov Chain algorithm as implemented in JAGS (Plummer, 2003). Under this framework, both environmental and residual correlations are represented as posterior distributions. Following Bayesian approaches, posterior distributions with 95% highest posterior density (HPD) intervals excluding zero indicate evidence for non-random association within a species pair. One JSDM was fitted to each dataset and plot size, resulting in four models for the AlpineM dataset, two models for the AlpineCM dataset, and three models for both the ArcticCM and the ArcticM datasets (first 12 rows in Table 1). The environmental variables were included both as linear and second-order terms to account for quadratic effects. All models included random effects on species and sites. To account for the hierarchical nested sampling design of the AlpineCM dataset (0.04 m² subplots nested within 4 m² sites, see Figure S4 in Appendix) and the Arctic datasets (plots within grids, see Figures S5–S7 in Appendix), we further added nested random effects (see Hui, 2016) to indicate which (sub)plot belongs to which plot/grid. Models were run with one chain (as recommended to deal with the sign switching issue; Hui, 2016), with a burn-in of 40,000 and additional 20,000 iterations. Chains were thinned every 20 iterations. Number of latent variables were set to three based on preliminary sensitivity analyses, yet the results did not fundamentally change with different number of latent variables. We used weakly informative priors for all parameters: a normal distribution with mean of zero and standard deviation of 10 for latent variable coefficients, species intercepts and species coefficients related to environmental variables. We used half-Cauchy distributions for standard deviation parameters associated with random effects on sites (Gelman, 2006). Convergence was assessed using the Geweke convergence diagnostic (Geweke, 1992), which is a diagnostic applicable with only one MCMC chain (see Table 1 in Appendix).

From model outputs, we evaluated the goodness-of-fit of the model using the True Skill Statistic (TSS; Allouche, Tsoar, & Kadmon, 2006). Specifically, we generated replicated presence-absence datasets using the joint posterior distribution of model parameters and computed TSS for each species and each sample of the posterior distribution. The overall fit of the model was evaluated by averaging TSS values across species. This procedure was repeated also for a set of 'environment-only' models which did not include latent variables, and thus assess the ability of abiotic factors alone to explain the distribution of species. TSS varies between -1 and 1, where 1 indicates a perfect model, 0 indicates no better than a random model and -1 indicates a perfectly wrong model.

2.3 | Additional datasets and models

We run additional models to examine the robustness of our results. First, the residual correlations, and thus the interpretation of biotic interactions, are contingent upon the environmental variables included within the model. In addition to missing factors (Hui, 2016;

Pollock et al., 2014), model residuals and thus their correlations can arise from scale mismatch between response and predictor variables. This issue is typical for datasets modelled with a spatial approach (Guisan & Thuiller, 2005) where environmental data usually present a coarser resolution than species data (Connor et al., 2018; Guisan, Graham, Elith, & Huettmann, 2007). For example while species data were collected at different plot sizes, environmental data had a resolution of 25 m for all alpine datasets and a resolution of 1 m² for ArcticCM dataset. To test how the scale mismatch affects the obtained results, we re-modelled the ArcticM dataset using a 16 m² resolution for environmental data for all models and plot sizes (1, 4 and 16 m²). TSS and environmental and residual correlations derived from the ArcticM (matching spatial resolution between species and environmental data) and ArcticM_{env16} datasets (non-matching spatial resolution) were then compared.

Second, in the original model of Araújo and Rozenfeld (2014), species datasets with a coarser resolution were formed by merging adjacent smaller sampling units into larger cells (as in the ArcticM dataset). Analyses of data where plots of different sizes are equal in number (i.e. nested so that larger cell contain information of only one cell of smaller size; as in the AlpineM and the ArcticCM datasets) may provide a different picture for scale dependency (Turner, O'Neill, Gardner, & Milne, 1989; Zurell et al., 2018). In addition, for JSDMs, the number of sites can influence model outputs by modifying the complexity of input data (i.e. higher *n*). To test for these effects, we re-modelled the ArcticM dataset but retained only 210 plots at each resolution. This was done so that four 1 m² plots in the centre of each 16 m² plot were combined to form a 4 m² plot, while one 1 m² plot located at the bottom-right corner of each 4 m² plot was chosen to form the 1 m² plot size (Figure S7 in Appendix). Environmental and residual correlations were then compared between the ArcticM and the ArcticM₂₁₀ datasets.

3 | RESULTS

All models converged well (on average more than 95% of the parameters converged; Table S1 in Appendix). The TSS indicates an overall good model performance for all datasets (*M* = 0.58; *SD* = 0.12; Table S1 in Appendix).

For most datasets and plot sizes, the majority of the species pairs presents 95% HPD intervals of environmental and/or residual correlations that exclude zero (i.e. indicating non-randomly associated species pair; Figure 2). Residual correlations are in general more common and stronger than environmental correlations, and positive residual correlations are more frequent and stronger than negative residual correlations (Figures 2 and 3).

For half of the datasets (AlpineM, ArcticCM and ArcticM₂₁₀), increasing plot size results in more species pairs for which environmental correlations are non-random (i.e. 95% HPD interval excluding zero; Figure 2). For these three datasets, the median absolute environmental posterior correlation stays rather stable with increasing plot size (Figure 3). Opposite results were obtained for

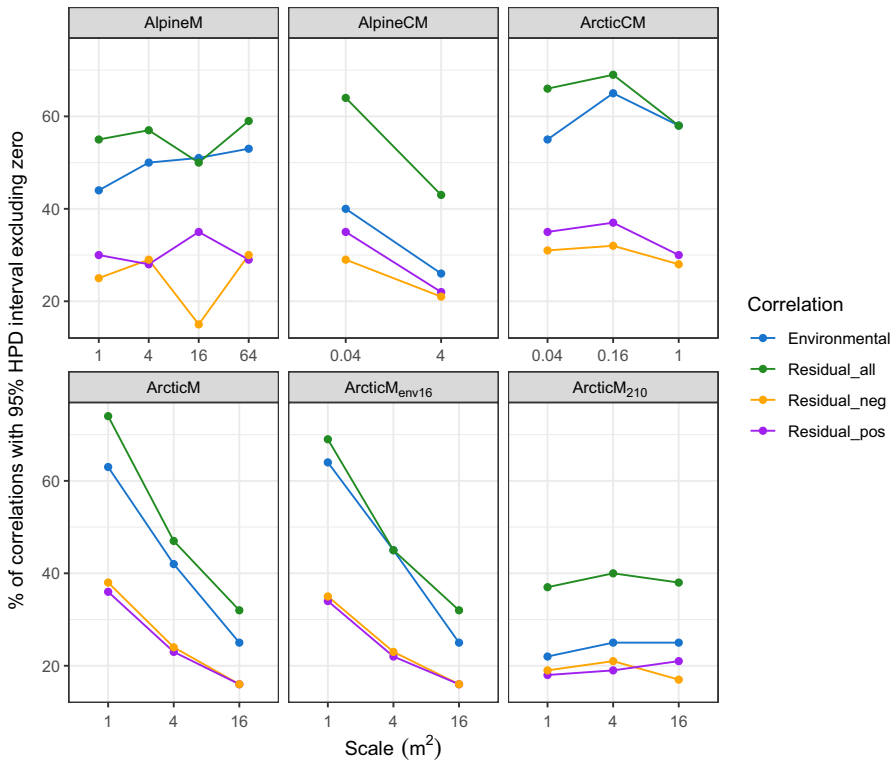


FIGURE 2 Percentages of species pairs attributed to environmental filtering (i.e. environmental correlation) and biotic interactions (i.e. residual correlation) across resolutions and datasets. A species pair is accounted as non-randomly associated if 95% highest posterior density interval of correlations does not overlap zero. Positive (aggregation) and negative (segregation) associations are determined by the sign of posterior median residual correlation [Colour figure can be viewed at wileyonlinelibrary.com]

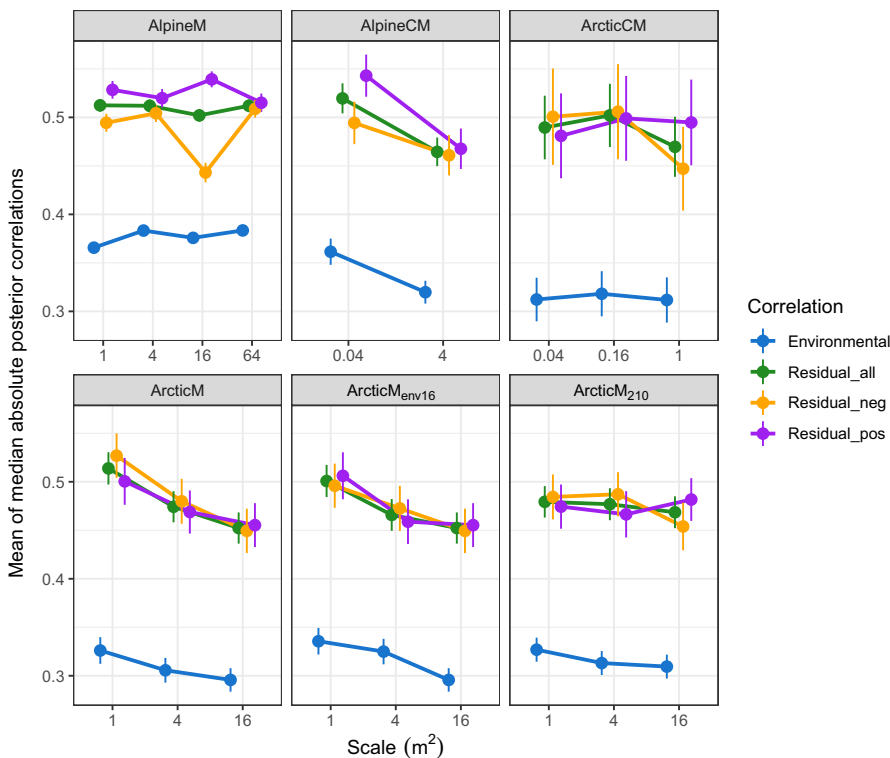


FIGURE 3 Absolute environmental and residual correlations among species pairs—indicating the strength of environmental filtering and biotic interactions respectively—across resolutions and datasets. Dots represent the average of the posterior median of absolute correlations across species pairs, while vertical bars represent the associated 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

the remaining datasets (AlpineCM, ArcticM, ArcticM_{env16}) with a decrease in both the proportion and the strength of non-random environmental associations. According to the TSS values of environment-only models, the abiotic predictors better explain the distribution of species at coarser than finer scales of all datasets (Table S1 in Appendix).

Percentages of species pairs with random/non-random residual correlations (i.e. 95% HPD interval overlapping/excluding zero) and median absolute residual posterior correlations do not vary consistently across plot sizes among datasets (Figures 2 and 3), but incorporating latent variables into the models improves TSS values more at fine than coarse scales for all datasets (Table S1 in Appendix).

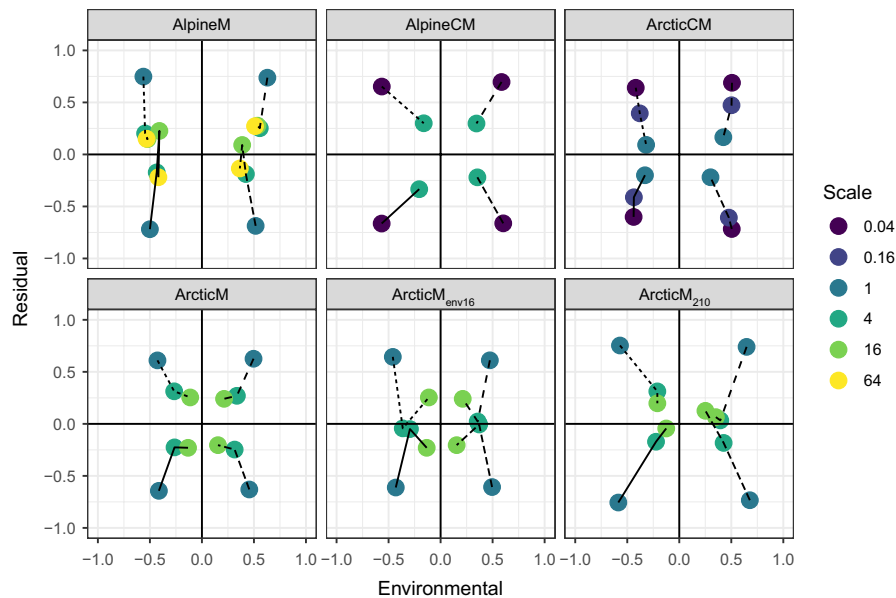


FIGURE 4 Shift of negative and positive environmental versus residual correlations across scales. The figure is computed by first choosing only species pairs that had non-random (95% highest posterior density [HPD] interval of correlations excluding zero) residual correlation at the finest scales. The species pairs were then assigned to the quadrats by environmental and residual correlations at the finest scale (top-left: negative environmental and positive residual correlations; top-right: positive environmental and residual correlations; bottom-left: negative environmental and residual correlations; and bottom-right: positive environmental and negative residual correlations). Finally, the mean environmental and residual correlations (shown as dots) across species pairs were calculated separately for each group of species pairs (i.e. based on their location in the quadrats at the finest scales). Lines of different type allow to connect the dots that belong to the same species pairs' group. Random associations (95% HPD interval of correlations overlapping zero) at the other than the finest scales were transformed to zero before calculating the means [Colour figure can be viewed at wileyonlinelibrary.com]

Distinguishing between negative and positive residual correlations (based on the sign of median of 95% HPD interval excluding zero) do not demonstrate large differences in the percentage or strength of association of species pairs across scales (Figures 2 and 3). However, the species pairs that have non-random negative residual correlation at the finest scales have weaker (or even positive for AlpineM and ArcticM₂₁₀ datasets) mean residual correlation at coarser scales than the species pairs that have non-random positive residual correlation at the finest scales (Figure 4).

Comparison between ArcticM and ArcticM_{env16}, the datasets with matching and non-matching spatial resolution between species and environmental data, shows only slight differences in environmental and residual correlations. Model fits of ArcticM_{env16} are better than the model fits of ArcticM (Table S1 in Appendix). Using the same number of plots within each resolution (ArcticM₂₁₀) results in less species pairs with non-random environmental correlations and less variation in residual correlations across scales.

4 | DISCUSSION

Scale dependency of assembly rules can affect the interpretations of factors driving the composition of communities (Götzenberger et al., 2012). In theory, it is frequently assumed that the process of environmental filtering mainly functions at spatial resolutions coarser than those at which biotic interactions act (Pearson & Dawson, 2003).

However, mixed results can be found in the literature, especially concerning the scale dependency of biotic interactions (Araújo & Luoto, 2007; Firth & Crowe, 2010; Reitalu et al., 2008). Recently, Araújo and Rozenfeld (2014) proposed that the type of biotic interactions should determine their scale dependency: negative interactions would be more apparent at small observational units with diminishing effects towards coarser scales, while positive interactions between species could be detected across spatial scales. Here, using empirical datasets together with JSDM, we tested these two hypotheses of scale dependency by investigating: (a) if the roles of environmental filtering and biotic interactions vary oppositely across scales, and (b) whether the scale dependency of biotic interactions vary depending on the type of interaction considered (i.e. positive or negative). We found partial support for the two above-mentioned hypotheses, but large variations exist depending on the dataset considered. Overall, due to the correlative nature of the applied methodology, the results must be interpreted only as indication of putative assembly rules (environmental filtering and biotic interactions) and their variation across spatial scales.

Regarding the first hypothesis, the analysis of environmental and residual correlations across scales indicates a somewhat strengthening and reduced role of environmental filtering and biotic interactions, respectively, with increasing plot size. The differences in percentages of species pairs with random/non-random environmental correlation and median absolute environmental correlations between scales are moderate and varied across datasets

(see Figures 1 and 2). The scale dependency of ecological assembly rules is better supported when looking at the model fits (i.e. how well the distribution of species is explained by abiotic predictors and latent variables). Fits of environment-only models improve with increasing plot size, and incorporating latent variables (i.e. surrogate to biotic interactions) improve model fits more at fine than at coarse scales. However, we acknowledge that the here-measured potential influences of environmental filtering and biotic interactions across scales could be related to the chosen environmental variables. For consistency, we used the same environmental predictors to model species data at all plot sizes for a given dataset. While these predictors are ecologically justified (Mod et al., 2016), depending on the scale, other abiotic factors might be more relevant (Yeager, Deith, McPherson, Williams, & Baum, 2017). For example, Belmaker et al. (2015) observed no significant variation in environmental filtering across scales when using the same set of environmental predictors to model bird occurrences, whereas Conti et al. (2017) found evidence for environmental filtering even at micro-scales (50 cm × 50 cm) when focusing on environmental heterogeneity instead of mean environmental conditions. Finally, the used plots are relatively small in size, and the scale dependency might have become more apparent if larger plot sizes or spatial extent (i.e. areal coverage as a component of scale) had been considered (see Viana & Chase, 2019).

The absolute overall residual correlations show no clear scale dependency, possibly due to the higher prevalence of species at larger plot size (see also Zurell et al. (2018), who demonstrated that species prevalence can drive the magnitude of residual correlations in JSDMs), and/or the stronger role of stochastic processes at fine scales (Bowman & Swatling-Holcomb, 2018). However, the differences in residual correlations across scales become more apparent when examining negative and positive residual correlations separately, as postulated in our second hypothesis based on the model of Araújo and Rozenfeld (2014). Especially negative associations occurring at the finest scales weaken slightly more than positive associations with increasing plot size for the majority of the datasets. This is especially the case for the species pairs that indicate competition due to the shared niche (i.e. have positive environmental correlation and negative residual correlation; see Table 2 and Figure 4). Different scale dependency of negative and positive biotic interactions might explain why the effect of biotic interactions have been demonstrated even at continental scales such as the effect of host on the distribution of a butterfly species (Araújo & Luoto, 2007), whereas evidence of negative interactions (competition, predation, amensalism) is mainly captured at fine scales (Purves & Law, 2002); but see Louthan, Doak, and Angert (2015) for the competitive exclusion acting at large spatial and temporal scales. Our results further indicate that the variances in the magnitude of residual correlations across scales were in general weak. This could be due to the effect of the 'stress-gradient hypothesis' (SGH; sensu Maestre, Callaway, Valladares, & Lortie, 2009) confounding the scale dependency of biotic interactions. The SGH postulates that positive biotic interactions should prevail over negative ones under harsh environmental

conditions (He, Bertness, & Altieri, 2013), and that the outcome of species pairwise interactions can vary from negative to positive with increasing environmental stress (Mod, le Roux & Luoto, 2014). The fact that our analyses are based on data from environmentally harsh high-latitude/-altitude study areas could diminish our ability to detect the scale dependency of negative biotic interactions (see also D'Amen et al., 2018).

Matching spatial resolution between species and environmental data (ArcticM dataset) do not considerably change the strength and the prevalence of environmental or residual correlations relative to the dataset with non-matching resolution (ArcticM_{env16}). This finding suggests that the scale mismatches should not affect environmental and residual correlations of Alpine and ArcticCM datasets either. However, model fits (as measured with TSS) of both environment-only and environment + residuals models were better for ArcticM_{env16} than ArcticM. This finding is against the expectations and calls for further studies of appropriate resolution for environmental data when studying assembly processes (see also Connor et al., 2018).

The second additional test, where the number of smaller plots was cut down to equal the number of largest plots (ArcticM₂₁₀ vs. ArcticM datasets), results in lower amount of species pairs with environmental correlation and less variation in both environmental and residual correlations across scales. There are more non-randomly associated species pairs at resolutions containing more plots, and this pattern is also visible for the AlpineCM dataset that has varying number of plots across sampling resolutions. Consequently, part of the results obtained with these datasets may actually stem from a methodological rather than an ecological phenomenon (see also Belmaker et al., 2015; Zurell et al., 2018). As the number of plots increases, so does the possibility to find associations between species by chance, possibly over-emphasizing aggregation and segregation patterns. Cutting down the number of plots (as done here for the ArcticM₂₁₀ dataset) does not seem to be the unsurpassed solution either, as it artificially removes ecological information from the dataset, but future applications of JSDM might need to include a penalization for datasets with higher *n*.

5 | CONCLUSIONS

Taken together, our results provide some support for the hypotheses related to the scale dependency of assembly rules. The role of environmental filtering and biotic interactions in structuring species assemblages did not consistently vary across scales, but the scale dependency of biotic interactions was revealed when partitioning the residual correlations into positive and negative associations. Influence of negative interactions decreases slightly more than the influence of positive interactions towards coarse spatial scales. Despite all datasets not unambiguously supporting the hypothesis, the generality of our findings is increased by the matter that we used datasets from two different study areas, in both alpine and arctic environments.

While we found JSDM as an efficient tool to disentangle the roles of ecological assembly rules across scales, it is conditional to the challenges of using statistical methods to infer patterns from empirical data: measured correlations can support but not prove causality (Dormann et al., 2012). Thus, JSDMs only indicate that environmental filtering and biotic interactions are potential causes of species aggregation and segregation. Further, and as previously identified (Pollock et al., 2014; Zurell et al., 2018), we detected that species prevalence, missing or inaccurate environmental predictors and data structure are potential sources of inaccuracy with JSDM. Thus, while our results are in line with a study based on simulated data (Zurell et al., 2018), we cannot assess the veracity of our findings (as is the case for many studies) due to a global lack of knowledge on assembly rules, especially biotic interactions, actually taking place in nature. The challenge remains to conduct studies across a multitude of communities, environmental conditions and spatial scales to comprehensively understand the role of ecological assembly rules in community building.

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AUTHORS' CONTRIBUTIONS

H.K.M. conceived the initial idea and led the writing, with all the authors contributing; M.L. and A.G. led the collections of the data; H.K.M. and M.C. analysed the data.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.1c59zw3sf> (Mod, Chevalier, Luoto, & Guisan, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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